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Research Article

Importance of woody patches and vegetation heterogeneity in Texas tortoise microhabitat use

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Microhabitat sites provide important resources and thermal conditions to reptile species that can vary spatially and temporally. This study assessed Texas tortoise *Gopherus berlandieri* microhabitat use and its relationship with carapace temperature during their active (April–October) and inactive seasons (November–March) between January 2023 and February 2024 in a thornscrub savanna in southern Texas, USA. Other studies have examined Texas tortoise microhabitat associations during the active season, but none have assessed these associations during months when they are inactive, a period important to their survival throughout the year. To do this, we collected ground cover and overhead canopy cover data at locations of telemetered tortoises and paired random locations. We compared microhabitat variables by location type to determine if tortoises associated with certain cover types. Then, we assessed the relationship between microhabitat variables at tortoise locations and carapace temperature using linear mixed models. Results indicated that carapace temperature was most strongly influenced by hour of day year-round and air temperature during the inactive season rather than associated microhabitat cover types year-round. Tortoises associated with higher values of woody-stemmed vegetation ground cover and overhead canopy cover than were available at random locations during both seasons. In addition to the importance of woody vegetation, the data suggest that tortoises most often used microhabitats with at least double the amount of grass and litter ground cover compared to other microhabitat variables. Managers prioritizing Texas tortoise conservation can use this information to manage vegetation to meet year-round needs of tortoises by aiming for variety in vegetation cover with woody patches dispersed throughout the landscape. Our findings highlight the importance of

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considering spatial and temporal microhabitat components that affect reptile success, such as the thermal properties and composition of available cover types, in conservation efforts.

Keywords: *Gopherus berlandieri*, habitat management, microhabitat, rangeland, reptile, telemetry, temperature, Texas, Texas tortoise, vegetation

Introduction

Habitat use studies are a key component in forming species conservation plans. Habitat is influential at various biological levels, including performance and function of an individual, population dynamics, and community interactions (Smith and Ballinger 2001, Rasmussen and Litzgus 2010, Todd et al. 2016). Understanding habitat relationships at multiple scales aids in recommending effective management actions for at-risk species. Macrohabitat associations (i.e. second order selection) are useful in conducting species surveys across a broader geographic range, while microhabitat associations (i.e. third order selection) examine more specific resource use and have utility in forming site management plans (Johnson 1980, Rasmussen and Litzgus 2010, Hibbitts et al. 2013).

Microhabitat studies provide important base knowledge for reptiles, which are declining globally (Mittermeier and Carr 1992, Gibbons et al. 2000, Tingley et al. 2016). For reptiles, microhabitat sites provide important resources including food, shelter, and thermoregulatory properties, and use of these resources can vary daily, seasonally, spatially, and across life stages (Bogert 1949, Rasmussen and Litzgus 2010, Todd et al. 2016, Elmore et al. 2017, Michael et al. 2017, Garrett et al. 2018). Testudines (turtles and tortoises) are particularly threatened: most species are classified at some level of conservation concern yet are underrepresented in conservation planning (Tingley et al. 2016, Roll et al. 2017, Lovich et al. 2018). Turtles and tortoises may use microhabitats based on vegetation attributes, temperature conditions, or a combination of the two (Grandmaison et al. 2010, Snyder 2014, Roe et al. 2019, Robertson et al. 2022).

Reptiles, including turtles and tortoises, behaviorally thermoregulate by selecting areas in their environment with suitable temperature conditions (microhabitats) and restricting activity periods to times when ambient temperatures are favorable, for example (Stevenson 1985, Grover 1996, Navas 1996, Scheffers et al. 2014, Shi et al. 2016, Ortega et al. 2019). Consequently, thermal conditions play a role in microhabitat selection and activity (Stevenson 1985, Grover 1996, Navas 1996, Ortega et al. 2019). Temperatures in microhabitats can vary predictably by vegetation structure. Certain vegetation classes, like shrub cover, for example, have cooling effects on surface temperatures because of their height and overhead obstruction of solar radiation (Londe et al. 2020). This may have implications for microhabitat selection by herpetofauna year-round, including periods of brumation (Ortega et al. 2019, Holden et al. 2021). Brumation is a means for ectotherms to survive periods of extreme cold. Conditions at brumation sites affect metabolic rate, energy storage, and overall body condition, which consequently affects the fitness and performance of an individual post-brumation (Ultsch 1989, Williams et al. 2015, Holden et al. 2021, Wilsterman et al. 2021). Thus, examining Testudines' microhabitat associations across space and time is critical to forming comprehensive conservation initiatives.

The Texas tortoise *Gopherus berlandieri* is listed as threatened by the state of Texas, where its range encompasses the southern portion of the state. Generally, Texas tortoises are known to use thornscrub vegetation communities in the Tamaulipan Biotic Province, a semiarid region characterized by growth of thorny shrubs, small trees, and cacti mixed with grasses and forbs (Blair 1950, Rose and Judd 2014). However, thornscrub savanna is a broad term that does not describe the finer scale variation in habitat conditions within this vegetation type across space. Thus, finer-scale assessments of Texas tortoise microhabitat use are necessary to make recommendations for management actions throughout their range to support their conservation.

Microhabitat studies have been conducted for Texas tortoises in a few different vegetation communities within the Tamaulipan Biotic Province in Texas. Studies have been conducted in the Rio Grande Plains ecoregion (Kazmaier et al. 2001a), the South Texas Plains ecoregion (Couvillon 2017), and coastal lomas (Briggs 2016). Texas tortoises strongly associated with areas containing woody plant cover in some capacity, selecting a broad range of canopy cover and closure and associating the least with areas on either extreme of that spectrum. More specifically, tortoises were least associated with areas devoid of woody vegetation or with closed canopies (Kazmaier et al. 2001a, Couvillon 2017). The tendency for Texas tortoises to associate with certain ranges of woody canopy cover while simultaneously utilizing a variety of vegetation types may indicate that thermal conditions play a role in space use. One study found a relationship between Texas tortoise carapace temperature and microhabitat substrate temperature, suggesting that thermal conditions may influence microhabitat use in this species (Couvillon 2017), and Texas tortoises on coastal lomas used prickly pear *Opuntia* spp. and rat midden cover when inactive, likely for thermal refugia (Briggs 2016).

Previous research assessed Texas tortoise microhabitat associations during the months of the year when tortoises are active only (Kazmaier et al. 2001a, Briggs 2016, Couvillon 2017). Here, we assessed microhabitat associations for Texas tortoises during both their inactive (approximately November–March) and active (approximately April–October) seasons (Rose and Judd 1975, Kazmaier et al. 2001b) on a coastal rangeland contained mostly within the Coastal Sand Plain

ecoregion. This information adds to the existing literature on Texas tortoise microhabitat associations and informs broader management by including information about the inactive season, which has never been examined. Microhabitat information during the active season is crucial for supporting important physiological processes such as foraging, breeding, and movement. However, microhabitat associations during the inactive season are also important to their physiology and for year-round management decisions. We also examined the relationship between tortoise carapace temperature and microhabitat variables to assess whether certain cover types provide different thermal conditions for Texas tortoises and if that relates to patterns of use. Our assessment of the spatial and temporal influences of vegetation cover and temperature conditions on microhabitat selection by Texas tortoises will provide valuable context for developing site management plans that prioritize reptile conservation.

Material and methods

Study area

We conducted this study on the East Foundation's El Sauz Ranch in Willacy and Kenedy Counties, TX, USA. The El Sauz Ranch comprises 10 984 ha of native semi-arid rangeland along the Texas Gulf Coast, adjacent to the Laguna Madre. This property contains a mixture of woodland, wetland, and grassland vegetation types. A majority (~ 60%) of the property occurs in the Coastal Sand Plain ecoregion, and the rest is evenly split amongst the Laguna Madre Barrier Islands and Coastal Marshes ecoregion and the Lower Rio Grande Valley ecoregion (Griffith et al. 2007, Baumgardt et al. 2019). Much of the study area could be described as a thornscrub savanna: most vegetation cover was herbaceous with thornscrub vegetation scattered throughout. Examples of common thornscrub species in the study area included honey mesquite *Prosopis glandulosa*, lotebush *Ziziphus obstusifolia*, granjeño *Celtis ehrenbergiana*, huisache *Vachellia farnesiana*, and prickly pear. Common herbaceous species included Gulf cordgrass *Spartina spartinae*, seacoast bluestem *Schizachyrium scoparium* var. *littorale*, crotons *Croton* spp., and many species from the family *Asteraceae*. This property was managed as a productive cattle *Bos taurus* ranch and as a working laboratory to study wildlife conservation and rangeland health. We collected our data in predefined areas, referred to as plots, that were subject to prescribed fire treatments as part of ongoing land management. These management activities likely contributed to variation in vegetation structure and microhabitat availability among plots. However, evaluating the effects of these management treatments are beyond the scope of this study.

Tortoise capture

From 2023 to 2024, we conducted meandering walking surveys and area searches throughout the property to locate and capture tortoises. We determined the age class (adult, juvenile) of captured tortoises using straight carapace length measured at the midline. Because secondary sexual characteristics are not reliably apparent in tortoises with a straight carapace length < 130 mm, we considered tortoises with a straight carapace length > 130 mm as adults (Judd and Rose 1989). Sexual dimorphism is visually apparent in adult Texas tortoises (Rose and Judd 2014); as such, we determined sex of adult tortoises based on carapace and plastron shape. Upon capture, we affixed a very-high frequency (VHF) transmitter (R2020 Reptile Glue-on, Advanced Telemetry Systems) in an off-center position along the rear costal scutes of each tortoise (Bernstein and Black 2005, Woodley 2013) using epoxy (SteelStik Epoxy Putty, JB Weld; Fig. 1). On the side opposite the transmitter, we attached an iButton temperature logger (DS1925, Maxim Integrated Products, Inc.) to collect carapace temperature data by adhering an iButton key ring mount (DS9093F, Maxim Integrated Products, Inc.) to a rear costal scute. The key ring mount allowed us to remove iButtons to download data regularly throughout the study period. The iButtons recorded temperature every hour throughout

Figure 1. Texas tortoise *Gopherus berlandieri* equipped with a very-high frequency radio transmitter (R2020 Reptile Glue-on, Advanced Telemetry Systems) on a rear costal scute on the left side of the carapace, an iButton temperature logger (DS1925, Maxim Integrated Products, Inc.) mounted in a key ring (DS9093F, Maxim Integrated Products, Inc.) on a rear costal scute on the right side, and a passive integrated transponder (PIT) tag (Biomark APT12, Merck and Co., Inc.) on a rear marginal scute on the right side. We adhered equipment to tortoises using epoxy (SteelStik Epoxy Putty, JB Weld) from 2023 to 2024 on a southern Texas rangeland, USA.

the study period. We adhered a passive integrated transponder (PIT) tag (Biomark APT12, Merck and Co., Inc.) to a rear marginal scute on the right side of each tortoise using epoxy for individual identification. We attached equipment comprising no more than 10% of the mass of an individual (Beaupre et al. 2004, Todd et al. 2016, Türkozan et al. 2019).

Microhabitat data collection

During their active and inactive seasons, we tracked tagged tortoises once/week to collect microhabitat information. We visually confirmed the location of each tortoise within plots and recorded microhabitat information at its location and 2 random paired locations. We generated random locations using a random number generator to produce a bearing (0–359°) and a distance ranging from 3 to 50 m from the tortoise location point. This range of distances produced random locations within a radius that tortoises could reasonably access based on their movement capabilities. We did not collect microhabitat information when a tortoise remained at the same location where it was found on the last visit to reduce non-independence of sampling points. We collected data seasonally: January–March 2023, June–August 2023, and January–February 2024. The data collection periods included two inactive seasons to increase sample size because tortoises moved much less frequently during winter months, resulting in fewer locations for sampling. We collected data between the morning and afternoon hours.

For all sampling locations, we recorded percentage ground cover values and percentage overhead canopy cover assessed from 1 m above the ground (hereafter collectively referred to as microhabitat variables). To determine percentage ground cover data, we used a modification of the Daubenmire (1959) method: we placed a 1-m^2 quadrat around the approximate center of the sampling location and visually estimated percentage values for broad functional cover types: grass, forb, woody-stemmed vegetation, litter, and bare ground. Litter ground cover included all detached, dead plant material, including but not limited to loose, dead herbaceous material, bark, twigs and branches, and logs. We estimated percentages to the nearest 5%, and all percentages for one sampling location totaled 100%. For overhead canopy cover, we used the mobile application Percentage Cover (Mignanelli 2018) to photographically measure percentage overhead canopy cover with the camera pointed skyward 1 m above the ground. We included all vegetation visible in the photographs in our canopy cover measurements, including leafless branches commonly encountered during the inactive season.

We included additional variables at tortoise locations for use in regression models: carapace temperature, activity status (active season only), daily average air temperature, and hour of day. Carapace temperature was recorded by the iButton temperature loggers every hour, so we used the temperature recorded closest in time (within 30 min) to the time we tracked a tortoise. Activity status (active, inactive) was only applicable during the active season data because we never observed a tortoise to be active in the winter (i.e. inactive season). Tortoises walking, feeding, interacting with other tortoises, or otherwise out from under cover were considered active, and tortoises in pallets (shallow impressions excavated in substrate) or under cover were considered inactive (Rose and Judd 2014). We downloaded daily average air temperatures from the Port Mansfield, Texas weather station (26°33′12″ N, 97°25′40″ W; ~ 5.5 km from study site) available in the NOWData records (National Weather Service, www.weather.gov/wrh/Climate?wfo=bro) and converted values from degrees Fahrenheit to degrees Celsius. Hour of day was the numerical value representing the hour in which a sampling location was measured.

Analysis

We compared microhabitat variables at tortoise (i.e. used) locations to random (i.e. available) locations with permutational multivariate analysis of variance (PERMANOVA; Anderson 2001) with the 'vegan' package (Oksanen et al. 2020) in R ver. 4.1.2 (www.r-project.org). We used 999 permutations and Bray–Curtis distance matrix. The microhabitat variables were the response variables, and location type was the predictor variable. The distributions of the microhabitat variables (grass, forb, woody-stemmed vegetation, litter, bare ground, and overhead canopy cover) did not meet the assumptions of normality; thus, we used nonparametric statistical methods. We analyzed data separately by season because tortoise behavior differs greatly during their active season versus their inactive season (Auffenberg and Weaver 1969, Rose and Judd 1975, Kazmaier et al. 2001b). We assessed significance at the $\alpha = 0.05$ level. To visualize and further explore differences between random and tortoise locations, we performed nonmetric multidimensional scaling (NMDS) with a Bray–Curtis distance matrix on the microhabitat variables (Kruskal 1964). We determined the number of dimensions to include using stress plots. We plotted the NMDS ordinations with vectors showing the direction and strength of influence of each microhabitat variable on the data points. We included 95% confidence ellipses for grouping variables (sampling location type) in the ordinations. Next, to assess if the distributions of each microhabitat variable varied by location type, we used two-sided Wilcoxon rank-sum tests, a nonparametric univariate analysis (Wilcoxon 1945, Mann and Whitney 1947). Although random locations were generated in association with each used location, we treated used and random points as independent samples for the Wilcoxon rank-sum tests to compare cover at used sites with overall microhabitat availability within the study area. With the active season data, we also ran the same analyses to assess the effect of tortoise activity status on microhabitat variables at tortoise locations only. In the models, 'active' served as the reference level, so parameter estimates indicate the comparison of 'inactive' to 'active'.

To examine the relationship between microhabitat use and tortoise microclimate, we investigated how tortoise carapace temperature related to microhabitat cover at tortoise locations using linear mixed models (LMM) in the R package 'lme4' (Bates et al. 2015). We produced separate models for each season with carapace temperature as the response

variable. The predictor variables included microhabitat variables, activity status (active season only), hour of day, and daily average air temperature. Though we were interested in the effects of vegetation (microhabitat variables) on carapace temperature, we included the other predictor variables in each model because we wanted to account for their effects on carapace temperature. For the microhabitat variables, we used all cover variables except forb. Because the ground cover variables sum to 100%, we removed one from the models, and forb appeared to be the least influential cover variable at tortoise locations during both seasons based on the NMDS ordinations.

We produced a set of candidate models using various combinations of microhabitat predictor variables. To develop the candidate sets, we evaluated numerous biologically plausible combinations of the measured microhabitat variables. The candidate model sets presented herein include the subset of models representing the primary biological hypotheses evaluated, rather than every model examined during preliminary exploratory analyses. We ranked the candidate models using Akaike information criterion corrected for small sample sizes (AIC_c) in order of ascending AIC_c value and descending model weight. To account for repeated measures across tortoises, we included a nested random effect of individual tortoise within plot in the active season models. We accounted for plot in the random effect term to account for potential differences in microhabitat characteristics among plots as a result of the prescribed fire and grazing treatments at the study site. In the inactive season models, we used the random effect of individual tortoise. We decided whether to use a nested or non-nested random effect for each season based AIC_c values, selecting the random effect type that resulted in lower values in models for each season. The candidate models had low AIC_c weights, indicating that no single model was a much better fit for the data than the other models; thus, we examined a confidence set of models, represented by the top models with a cumulative weight of ≤ 95% (Symonds and Moussalli 2011, Harrison et al. 2018). To verify that the assumptions of each confidence set of models were met, we examined residuals and used diagnostic plots, including QQ plots and residual plots. In LMMs, we considered parameter confidence intervals that did not contain zero as significant.

Results

Active season

We tracked 42 tortoises (20 males, 15 females, 7 juveniles) and collected microhabitat data at 214 tortoise locations and 428 random locations during the active season. The PERMANOVA results indicated that there were differences between microhabitat variables at tortoise locations and at random locations ($F_{1,640}$ = 56.0, R^2 = 0.081, p = 0.001). NMDS ordination (k = 3, stress = 0.082) indicated that overhead canopy cover and litter ground cover had the strongest associations with tortoise locations (Fig. 2).

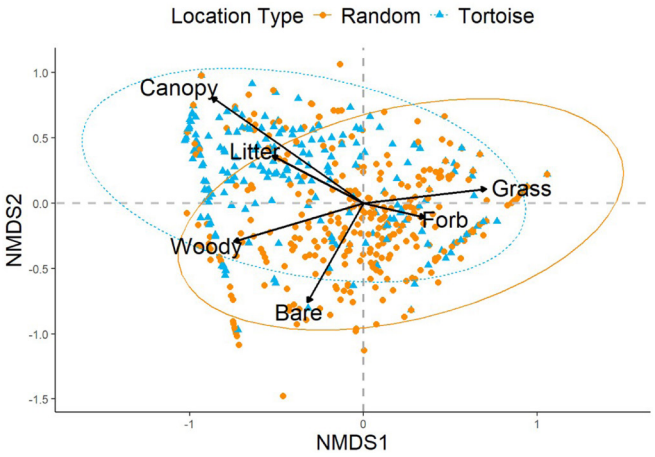

Figure 2. Non-metric multidimensional scaling (NMDS) ordination of active season (June–August) microhabitat use by Texas tortoises *Gopherus berlandieri*, grouped by sampling location type in southern Texas, USA, 2023. Texas tortoise locations are represented by blue triangles and random locations are represented by orange circles. The dashed and solid lines represent 95% confidence ellipses around the tortoise locations and random locations, respectively. Arrow vectors indicate strength and direction of the effect of each microhabitat variable on the ordination and are labeled with the corresponding variable.

Wilcoxon rank-sum tests showed differences in distributions of grass, forb, woody-stemmed vegetation, litter, and overhead canopy cover by sampling location type (Table 1). Tortoises used all cover types, though distributions of each cover type varied (Table 1, Fig. 3). Interquartile ranges for cover variables at tortoise locations were 0–55% grass, 0–10% forb, 0–20% woody stem cover, 10–60% litter, 0–25% bare ground, and 0–61% overhead canopy cover (Fig. 3). These ranges indicate quantities of each variable most often used by tortoises. Compared to random locations, tortoises associated with higher values of litter, woody-stemmed vegetation, and overhead canopy cover and lower values of grass and forb cover (Table 1). There was no difference in bare ground values between tortoise and random locations (p = 0.29).

The PERMANOVA of microhabitat variables as a function of tortoise activity status indicated no difference in microhabitat variables at locations where they were active compared to where they were inactive ($F_{1,212}$ = 1.08, R^2 = 0.005, p = 0.32). NMDS (k = 3, stress = 0.089) ordination showed no clear grouping by activity status with confidence ellipses completely overlapping. Wilcoxon rank-sum tests assessing individual microhabitat variables only showed a difference in forb use when tortoises were active compared to inactive (W = 5560.5, p = 0.005), with active tortoises using more forb cover ($\bar{x}_{active}$ = 7.5 ± 9.2, $\bar{x}_{inactive}$ = 5.7 ± 11.0).

We produced 15 candidate LMMs with 126 tortoise locations from the active season. Before producing models, we removed 19 observations when tortoises were observed in a hole/burrow below the surface, as that negates direct effects of vegetation cover on carapace temperature. Carapace temperatures during the active season ranged from 21.0 to

Table 1. Univariate nonparametric tests (Wilcoxon rank-sum) comparing the distributions of microhabitat variables (percentage ground cover variables, percentage overhead canopy cover) at Texas tortoise *Gopherus berlandieri* locations (t) and random locations (r) for the active (June–August) and inactive (January–March) seasons in southern Texas, USA, 2023–2024. Medians (med) and means ($\bar{x}$) for each location type are listed with the W statistic and p-value from the models. Significance at the $\alpha = 0.05$ level is indicated by *.

	Microhabitat variables					
Active season	%Grass	%Forb	%Woody stem	%Litter	%Bare	%Canopy
med_t/med_r	25/50	0/5	5/0	30/5	10/10	24/0
$\bar{x}_t/\bar{x}_r$	31.3/48.4	6.2/9.6	10.5/6.1	36.6/16.3	15.4/19.6	31.1/5.9
W	58 956	53 032	32 731	25 247	48 100	23 191
p-value	< 0.001*	< 0.001*	< 0.001*	< 0.001*	0.286	< 0.001*
Inactive season	%Grass	%Forb	%Woody stem	%Litter	%Bare	%Canopy
med_t/med_r	40/30	5/5	8/0	15/15	5/20	0/0
$\bar{x}_t/\bar{x}_r$	39.8/41.5	6.3/8.3	15.9/5.4	28.8/22.0	9.2/22.9	25.7/9.6
W	3780	3964	2262	3197	4512	2826
p-value	0.584	0.249	< 0.001*	0.217	0.005*	0.004*

42.5°C. Daily average air temperatures during the active season ranged from 25.6 to 33.1°C. The confidence set of models met the assumptions of normality and homogeneity of variance. The top-ranking model included activity status, hour of day, and daily average air temperature, without microhabitat variables, as predictor variables (Table 2). Hour of day had the greatest effect on carapace temperature, forming a positive relationship (Table 3). Among the top models, the passing of an hour corresponded with a carapace temperature increase of 2.07–2.13°C. Activity status had the next strongest effect: inactive tortoises had carapace temperatures 1.34–1.48°C cooler than active tortoises. Although overhead canopy cover was present in 7 of the 10 models in the candidate set, the cumulative model weight was only 0.49 (Table 2) and parameter confidence intervals always overlapped with zero (Table 3). Overhead canopy cover, grass, bare ground, litter, and woody stem cover did not clearly affect tortoise carapace temperature.

Inactive season

We tracked 37 tortoises (21 males, 14 females, 2 juveniles) and collected microhabitat data at 60 tortoise locations

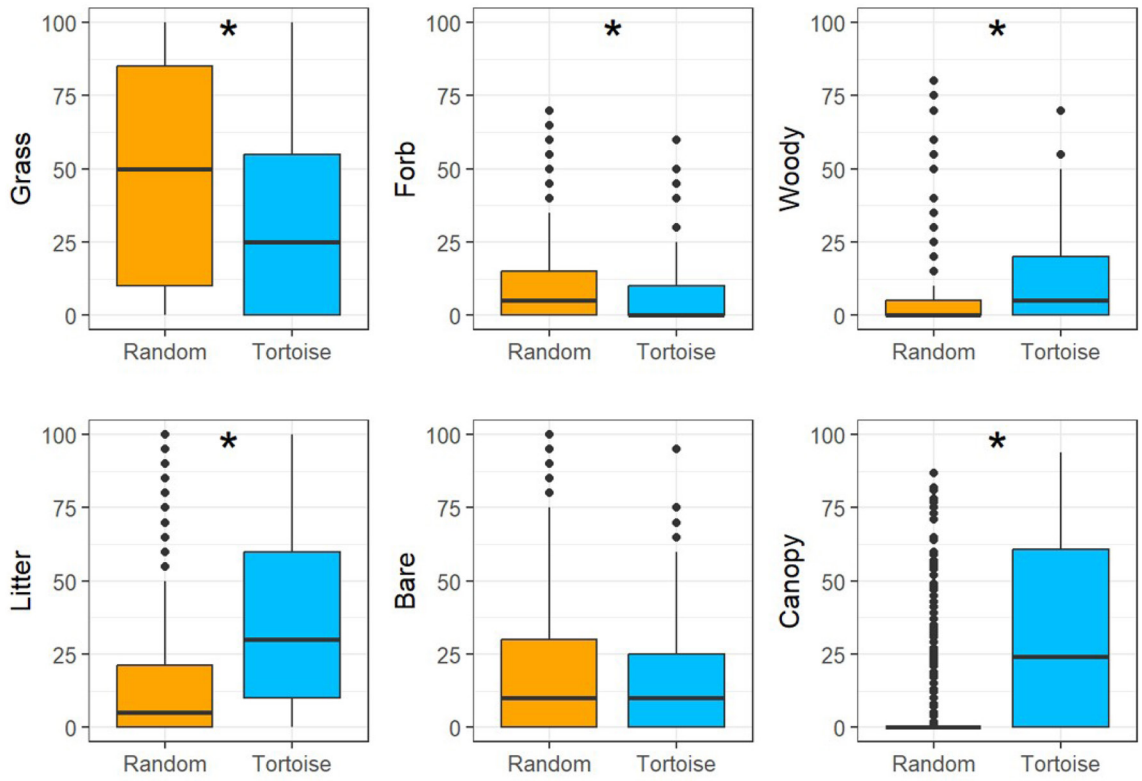

Figure 3. Percentage of ground cover variables (grass, forb, woody stem, litter, bare) and overhead canopy cover at randomly sampled locations (left, orange) and Texas tortoise *Gopherus berlandieri* locations (right, blue) during the active season (June–August) in southern Texas, USA, 2023. Asterisks (*) indicate cover types that differed between random and tortoise locations in Wilcoxon rank-sum tests.

Table 2. Confidence set of candidate linear mixed models, which account for the top 95% cumulative AIC_c weight from the original 15 candidate models. Models assess the effects of the listed predictor variables on Texas tortoise *Gopherus berlandieri* carapace temperature (°C) in the active season (June–August), along with the nested random effect of individual tortoise within predefined plots in the study area in southern Texas, USA, 2023. Predictor variables include hour of day, daily average air temperature (°C), activity status (active, inactive), percentage ground cover variables, and percentage overhead canopy cover. Values shown are degrees of freedom (DF), the log-likelihood value (logLik), Akaike information criterion corrected for small sample sizes (AIC_c), difference in AIC_c value compared to the lowest AIC_c value (ΔAIC_c), individual model Akaike weights (weight), and cumulative Akaike weights.

	Models	df	logLik	AIC_c	ΔAIC_c	Weight	Cumulative weight
1	Hour of day + Air temp + Activity status	7	−278.8	572.5	0	0.29	0.29
2	Hour of day + Air temp + Activity status + %Canopy	8	−278.2	573.7	1.22	0.16	0.45
3	Hour of day + Air temp + Activity status + %Bare	8	−278.5	574.3	1.77	0.12	0.57
4	Hour of day + Air temp + Activity status + %Canopy + %Grass	8	−277.8	575.1	2.61	0.08	0.65
5	Hour of day + Air temp + Activity status + %Canopy + %Litter	9	−277.8	575.2	2.68	0.08	0.73
6	Hour of day + Air temp + Activity status + %Canopy + %Bare	9	−278.1	575.7	3.21	0.06	0.79
7	Hour of day + Air temp + Activity status + %Canopy + %Woody stem	9	−278.2	576.0	3.51	0.05	0.84
8	Hour of day + Air temp + Activity status + %Bare + %Litter	9	−278.5	576.5	4.03	0.04	0.88
9	Hour of day + Air temp + Activity status + %Canopy + %Bare + %Litter	10	−277.5	576.9	4.40	0.03	0.91
10	Hour of day + Air temp + Activity status + %Canopy + %Woody stem + %Grass	10	−277.5	576.9	4.44	0.03	0.94

Table 3. Parameter estimates and the upper and lower limits of their 95% confidence intervals for effects of predictor variables on Texas tortoise *Gopherus berlandieri* active season (June–August) carapace temperature in each of the top 95% of candidate linear mixed models in southern Texas, USA, 2023. Predictor variables include hour of day, daily average air temperature (°C), activity status (active, inactive), percentage ground cover variables, and percentage overhead canopy cover. Parameters with significant slopes, where zero is not contained within the 95% confidence interval, are bolded. For activity status, 'active' served as the reference level. Empty cells indicate models where that parameter was not included.

		Model									
		1	2	3	4	5	6	7	8	9	10
(Intercept)	Est.	6.08	5.57	5.98	6.12	5.53	5.54	5.45	6.04	5.48	5.75
	2.50%	−3.05	−3.56	−3.10	−3.03	−3.55	−3.54	−3.79	−3.05	−3.54	−3.42
	97.50%	15.2	14.7	15.1	15.3	14.6	14.6	14.7	15.1	14.5	14.9
Hour	Est.	**2.07**	**2.11**	**2.07**	**2.1**	**2.11**	**2.1**	**2.12**	**2.06**	**2.1**	**2.13**
	2.50%	1.76	1.79	1.76	1.78	1.8	1.79	1.79	1.75	1.79	1.8
	97.50%	2.38	2.43	2.37	2.42	2.43	2.42	2.45	2.37	2.42	2.46
Air temp.	Est.	0.26	0.27	0.26	0.26	0.26	0.27	0.27	0.25	0.26	0.27
	2.50%	−0.05	−0.04	−0.05	−0.04	−0.04	−0.04	−0.04	−0.05	−0.04	−0.03
	97.50%	0.56	0.57	0.56	0.56	0.56	0.57	0.58	0.56	0.56	0.58
Activity status	Est.	**−1.48**	**−1.45**	**−1.45**	**−1.37**	**−1.39**	**−1.43**	**−1.45**	**−1.44**	**−1.35**	**−1.34**
	2.50%	−2.33	−2.30	−2.31	−2.23	−2.25	−2.28	−2.30	−2.30	−2.21	−2.21
	97.50%	−0.62	−0.60	−0.60	−0.50	−0.53	−0.58	−0.60	−0.58	−0.49	−0.48
Canopy	Est.		−0.01		−0.01	−0.01	−0.01	−0.01		−0.01	−0.01
	2.50%		−0.02		−0.03	−0.03	−0.02	−0.02		−0.03	−0.03
	97.50%		0.01		0.005	0.01	0.01	0.01		0.005	0.004
Bare	Est.			0.01			0.01		0.01	0.01	
	2.50%			−0.01			−0.02		−0.01	−0.01	
	97.50%			0.03			0.03		0.03	0.03	
Litter	Est.					0.01			0	0.01	
	2.50%					−0.01			−0.01	−0.01	
	97.50%					0.03			0.02	0.03	
Grass	Est.				−0.01						−0.01
	2.50%				−0.02						−0.03
	97.50%				0.01						0.01
Woody stem	Est.							−0.003			−0.02
	2.50%							−0.04			−0.06
	97.50%							0.03			0.03

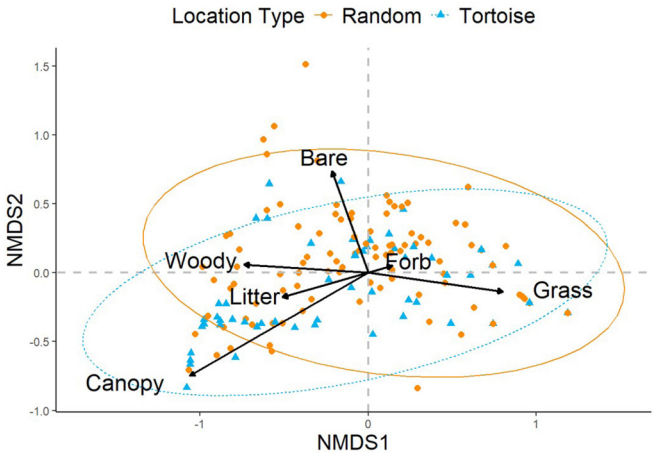

Figure 4. Non-metric multidimensional scaling (NMDS) ordination of inactive season (January–March) microhabitat use by Texas tortoises *Gopherus berlandieri*, grouped by sampling location type in southern Texas, USA, 2023–2024. Tortoise locations are represented by blue triangles and random locations are represented by orange circles. The dashed and solid lines represent 95% confidence ellipses around tortoise locations and random locations, respectively. Arrow vectors indicate strength and direction of the effect of each microhabitat variable on the ordination and are labeled with the corresponding variable.

and 120 random locations during the inactive season. The PERMANOVA results indicated that microhabitat variables differed between tortoise locations and random locations ($F_{1,178} = 6.33$, $R^2 = 0.034$, $p = 0.003$). NMDS ordination ($k = 3$, stress = 0.068) showed use of all cover types by tortoises, but overhead canopy cover showed the strongest association with tortoise locations (Fig. 4).

Wilcoxon rank-sum tests for each cover variable showed differences in distributions of woody-stemmed vegetation, bare ground, and overhead canopy cover between tortoise and random locations (Table 1). Tortoises used all cover types, but in varying quantities (Table 1, Fig. 5). Interquartile ranges for cover variables at tortoise locations were 0–69% grass, 0–10% forb, 0–25% woody stem cover, 5–56% litter, 4–11% bare ground, and 0–67% overhead canopy cover (Fig. 5). These ranges indicate quantities of each variable most often used by tortoises. Tortoises associated with higher values of woody stem and overhead canopy cover, but lower values of bare ground, than random locations (Table 1). There were no differences in grass, forb, or litter ground cover between location types during the inactive season.

For the inactive season LMMs, there were 51 data points with carapace temperatures. Carapace temperatures ranged from 5.5 to 40.5°C. Daily average air temperatures during the inactive season ranged from 3.6 to 25.0°C. We produced 15 candidate models. The confidence set of models met the assumptions of normality and homogeneity of variance. The top-ranking model included hour of day, daily average air temperature, bare ground, and woody stem cover (Table 4). Among the confidence set of models, the passing of an hour corresponded with a carapace temperature increase of 1.30–1.44°C (Table 5). Air temperature also formed a positive relationship with carapace temperature in the top models, corresponding with a 1.08–1.14°C increase in carapace temperature for each degree increase in air temperature. The cumulative model weight for woody stem cover

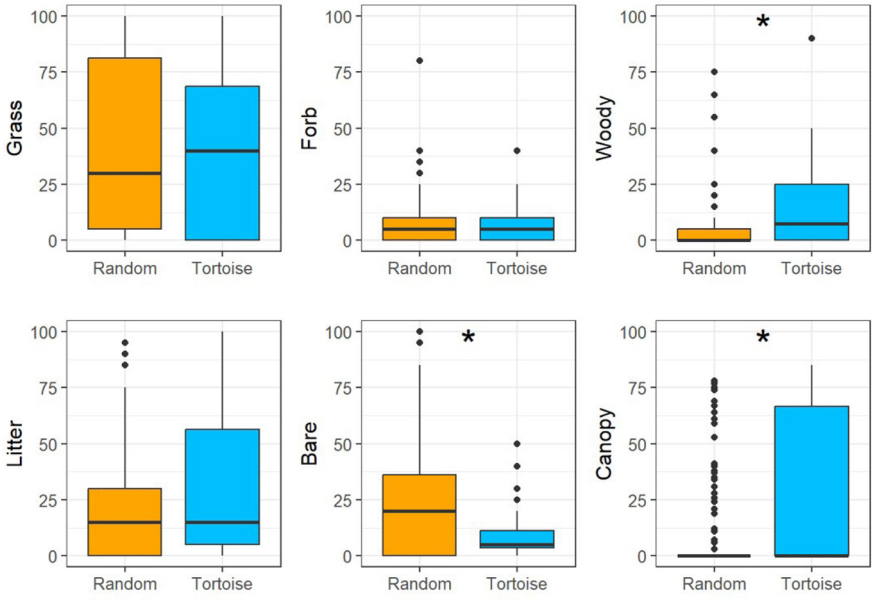

Figure 5. Percentage of ground cover variables (grass, forb, woody stem, litter, bare) and overhead canopy cover at randomly sampled locations (left, orange) and Texas tortoise *Gopherus berlandieri* locations (right, blue) during the inactive season (January–March) in southern Texas, USA, 2023–2024. Asterisks (*) indicate cover types that differed between random and tortoise locations in Wilcoxon rank-sum tests.

Table 4. Confidence set of candidate linear mixed models, which account for the top 95% cumulative AIC_c weight from 15 candidate models. Models assess the effects of the listed predictor variables on Texas tortoise *Gopherus berlandieri* carapace temperature recorded during the inactive season (January–March), along with the random effect of individual tortoise in the study area in southern Texas, USA, 2023–2024. Predictor variables include hour of day, daily average air temperature (°C), percentage ground cover variables, and percentage overhead canopy cover. Values shown are degrees of freedom (DF), the log-likelihood value (logLik), Akaike information criterion corrected for small sample sizes (AIC_c), difference in AIC_c value compared to the lowest AIC_c value (ΔAIC_c), individual model Akaike weights (weight), and cumulative Akaike weights.

	Models	df	logLik	AIC_c	ΔAIC_c	Weight	Cumulative weight
1	Hour of day + Air temp + %Bare + %Woody stem	7	−138.9	294.4	0.00	0.26	0.26
2	Hour of day + Air temp + %Woody stem	6	−140.6	295.1	0.74	0.18	0.44
3	Hour of day + Air temp + %Bare	6	−141.4	296.7	2.34	0.08	0.52
4	Hour of day + Air temp + %Canopy+ %Woody stem	7	−140.1	296.8	2.41	0.08	0.60
5	Hour of day + Air temp + %Litter+ %Woody stem	7	−140.1	296.9	2.48	0.08	0.68
6	Hour of day + Air temp	5	−142.8	297.0	2.60	0.07	0.75
7	Hour of day + Air temp + %Canopy + %Bare + %Woody stem	8	−138.8	297.1	2.69	0.07	0.82
8	Hour of day + Air temp + %Bare + %Litter + %Woody stem	8	−138.8	297.1	2.71	0.07	0.88
9	Hour of day + Air temp + %Canopy + %Bare	7	−141.2	299.0	4.61	0.03	0.91
10	Hour of day + Air temp + %Canopy + %Grass + %Woody stem	8	−139.8	299.1	4.69	0.03	0.93

was 0.77 (Table 4) and showed a negative relationship with carapace temperature, with models indicating a decrease in carapace temperature of 0.06–0.07°C for each percentage point increase in woody stem ground cover (Table 5). Although bare ground was present in 5 of the 10 models in the candidate set, the cumulative model weight was only 0.51 (Table 4) and parameter confidence intervals always overlapped with zero (Table 5). Grass, litter, bare ground, and overhead canopy cover did not clearly affect tortoise carapace temperature.

Table 5. Parameter estimates and the upper and lower limits of 95% confidence intervals for effects of the predictor variables on Texas tortoise *Gopherus berlandieri* carapace temperature during the inactive season (January–March) from a set of the top 95% of candidate linear mixed models in southern Texas, USA, 2023–2024. Predictor variables include hour of day, daily average air temperature (°C), percentage ground cover variables, and percentage overhead canopy cover. Parameters with significant slopes, where zero is not contained within the 95% confidence interval, are bolded.

		Model									
		1	2	3	4	5	6	7	8	9	10
(Intercept)	Est.	**−11.8**	**−11.4**	**−13.6**	**−10.5**	**−10.4**	**−13.3**	**−11.4**	**−11.4**	**−13.0**	**−9.25**
	2.50%	−18.6	−18.4	−20.5	−17.7	−17.7	−20.4	−18.4	−18.5	−20.1	−17.2
	97.50%	−4.98	−4.31	−6.76	−3.35	−3.17	−6.18	−4.44	−4.33	−5.86	−1.30
Hour	Est.	**1.34**	**1.32**	**1.44**	**1.3**	**1.3**	**1.44**	**1.33**	**1.33**	**1.43**	**1.32**
	2.50%	0.87	0.84	0.97	0.82	0.82	0.95	0.86	0.86	0.95	0.84
	97.50%	1.8	1.81	1.91	1.79	1.78	1.92	1.8	1.8	1.9	1.8
Air temp	Est.	**1.1**	**1.14**	**1.08**	**1.13**	**1.13**	**1.12**	**1.1**	**1.1**	**1.08**	**1.12**
	2.50%	0.88	0.91	0.85	0.9	0.9	0.88	0.87	0.87	0.84	0.89
	97.50%	1.33	1.37	1.31	1.36	1.37	1.35	1.33	1.33	1.31	1.35
Canopy	Est.				−0.02			−0.01		−0.01	−0.03
	2.50%				−0.05			−0.04		−0.04	−0.07
	97.50%				0.01			0.03		0.02	0.02
Bare	Est.	0.1		0.09				0.09	0.09	0.08	
	2.50%	−0.002		−0.01				−0.02	−0.02	−0.03	
	97.50%	0.2		0.2				0.2	0.2	0.19	
Litter	Est.					−0.02			−0.01		
	2.50%					−0.05			−0.04		
	97.50%					0.02			0.03		
Grass	Est.										−0.02
	2.50%										−0.07
	97.50%										0.03
Woody stem	Est.	**−0.06**	**−0.06**		**−0.06**	**−0.06**		**−0.06**	**−0.06**		**−0.07**
	2.50%	−0.11	−0.11		−0.11	−0.11		−0.11	−0.11		−0.14
	97.50%	−0.01	−0.01		0.00	−0.01		−0.01	−0.01		−0.004

Discussion

Our results show that Texas tortoises use a broad range of cover types during both their active and inactive seasons. This is the first time that microhabitat associations have been assessed during the inactive season for Texas tortoises. Microhabitat selection during the inactive season, when temperatures are cold and tortoises are in brumation, warranted exploration to determine if selection differed from that of the active season when temperatures are higher. However, because this study focused on a single Texas tortoise population during just one active season and two inactive seasons, our findings may not be generalizable to populations occupying habitats with different microhabitat availability (e.g. thornscrub-dominated areas). Studies longer in duration and across regions with varying vegetation cover are needed to clarify relationships found herein and better understand Texas tortoise ecology.

Texas tortoises used cover types and quantities that differed from the surrounding available microhabitat in this study, showing higher overall use of microhabitat variables associated with woody vegetation, including woody stem ground cover and overhead canopy cover, during both seasons. Microhabitat variables that differed at used and random locations varied seasonally, but Texas tortoises exhibited similar patterns of microhabitat use during both the active and inactive seasons despite behavioral activity differences during these times. Though we expected ground cover types and overhead canopy cover to influence carapace temperatures, we only found a significant relationship between woody stem ground cover and carapace temperature in the inactive season. Activity formed a stronger relationship with carapace temperature than microhabitat variables during the active season.

Year-round, tortoises used areas with greater values of overhead canopy cover and woody stem ground cover than were generally available. This association with woody vegetation is consistent with previous studies of Texas tortoise microhabitat use during their active season (Kazmaier et al. 2001a, Couvillon 2017). Other species in the genus *Gopherus* tend to associate with woody vegetation as well, including *G. morafkai* (Grandmaison et al. 2010, Todd et al. 2016), *G. polyphemus* (Tuberville et al. 2007, Yager et al. 2007, Hunter and Rostal 2021), and *G. flavomarginatus* (Lieberman and Morafka 1988, Lara-Reséndiz et al. 2024). The portion of the study area where we collected data consisted of plots managed via patch-burn grazing and was dominated by herbaceous vegetation (~ 44% of total cover) with intermixed woody vegetation (~ 36% of total cover), based on Rangeland Analysis Platform data (2023–2024; Jones et al. 2021, USDA Agricultural Research Service 2025). Although the plots differed in prescribed fire and grazing histories, evaluating the effects of these management practices on vegetation or Texas tortoise microhabitat use was beyond the scope of this study. Associations with higher overhead canopy cover, litter, and woody stem ground cover at tortoise locations thus suggest that patches of woody vegetation serve as important microhabitat sites for Texas tortoises year-round.

Although Texas tortoises generally selected microhabitats with greater woody stem ground cover and overhead canopy cover, they used all measured cover types in variable quantities throughout the year. This pattern suggests that different cover types likely have utility in facilitating different tortoise behaviors or seasonal needs. For example, some tortoises brumated in pallets created at locations containing some bare ground during the inactive season, indicating that suitable brumation sites can occur in microhabitats with bare ground. During the active season, tortoises also often used bare ground for traveling or basking during their peak activity periods during the day (pers. obs.). Additionally, though they used less grass and forb cover than was available to them during the active season, this herbaceous vegetation comprised the dominant cover type in the study area and, importantly, makes up a large part of their diet (Scalise 2011, Briggs 2016). Microhabitats used, even in lower quantities, can still provide useful resources to at-risk species (Walkup et al. 2019). Collectively, our data and field observations indicate that a landscape containing heterogeneity in vegetation types may provide the diversity in microhabitats required to support multiple aspects of Texas tortoise ecology throughout the year. Similar recommendations for providing variation in vegetation composition and structure have been made for other Testudines (Tuberville et al. 2007, Yager et al. 2007, Grandmaison et al. 2010, Todd et al. 2016, Hunter and Rostal 2021, Robertson et al. 2022, Lara-Reséndiz et al. 2024).

Because carapace temperature is related to microhabitat substrate temperature (Couvillon 2017), we were interested in assessing if cover types influenced carapace temperature. We did not find strong relationships between any specific cover type and carapace temperature during either season. Vegetation height and overhead cover have more direct influence on microhabitat temperature than vegetation composition itself, but certain cover types, like shrub cover, are strongly associated with these structural properties that directly affect microhabitat temperatures (Londe et al. 2020). Though overhead canopy cover and woody stem cover had negative relationships with carapace temperature in models where they were present, the only significant estimates were for woody stem cover during the inactive season (Table 2, 5). Our results could mean that tortoises manage their temperature using the structure of vegetation cover types available to them rather than seeking out a specific cover type consistently for its thermal properties. This emphasizes that heterogeneity in available vegetation cover and structure is important to Texas tortoise ecology.

Tortoise activity status during the active season affected carapace temperatures, though we did not find a difference in microhabitat associations between active tortoise locations and inactive tortoise locations. Previous work found that body temperatures of active Texas tortoises were more closely associated with air temperature, while inactive tortoise body temperature related more strongly to substrate temperature (Judd and Rose 1977). Although carapace temperature is not equivalent to internal body temperature, it reflects the

thermal conditions a tortoise experiences within the immediate microhabitat. Our results suggest that differences in carapace temperatures between active and inactive tortoises, despite similar vegetation associations, may relate more to how tortoises use the vegetation than to the vegetation type itself. Resting tortoises are typically concealed beneath the vegetation in their pallets, whereas active tortoises often move on top of or through vegetation, exposing themselves and the iButtons to increased solar radiation. Because we did not measure substrate temperature at individual tortoise locations, however, we could not directly compare carapace temperatures with the thermal conditions of occupied microhabitats.

The observed effect of activity status on carapace temperature may help explain why air temperature was a significant predictor in the inactive season models but not during the active season. During the active season, behavioral differences between active and inactive tortoises likely contributed sufficient variation in carapace temperature such that the influence of air temperature was reduced and thus insignificant in the models. In contrast, during the inactive season, tortoises were predominantly immobile while brumating. This consistent inactivity reduces behavioral variation and limits the influence of activity on carapace temperature, making air temperature a stronger predictor during that period. The intrinsic interaction between activity periods and microhabitat selection as forms of behavioral thermoregulation (Stevenson 1985, Grover 1996, Navas 1996, Ortega et al. 2019) is consistent with our results.

Our study contributes to the existing literature on Texas tortoise microhabitat associations by not only examining their active season preferences but also assessing their inactive season associations, which had not been previously explored. Our findings and the literature suggest that Texas tortoises use a broad range of vegetation types in southern Texas, emphasizing the importance of heterogeneity in vegetation as a management objective. Patches of woody vegetation provide important microhabitat sites for Texas tortoises within this thornscrub savanna ecosystem. Additionally, our data suggest that tortoises most often use microhabitats with at least double the amount of grass and litter ground cover compared to other variables. Therefore, land management plans should aim for a combination of herbaceous vegetation and patches of woody vegetation to effectively support the conservation of this state-threatened species.

The implications of our study extend beyond species-specific management. Our findings emphasize the utility of understanding spatial and temporal variation in microhabitat associations for forming site management plans and highlight the importance of addressing the diverse resource needs of reptile species to support their survival and persistence. By demonstrating how vegetation cover and temperature conditions influence microhabitat selection and carapace temperature throughout the year for Texas tortoises, this study underscores the critical need to integrate these factors into reptile conservation planning.

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Author contributions

Camryn M. Kiel: Conceptualization (lead); Data curation (lead); Formal analysis (lead); Investigation (lead); Methodology (lead); Project administration (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (equal). **Danielle K. Walkup**: Formal analysis (supporting); Methodology (supporting); Writing – review and editing (equal). **Sandra Rideout-Hanzak**: Conceptualization (supporting); Methodology (supporting); Writing – review and editing (equal). **Evan P. Tanner**: Conceptualization (supporting); Methodology (supporting); Writing – review and editing (equal). **Ashley M. Tanner**: Conceptualization (supporting); Methodology (supporting); Writing – review and editing (equal). **Andrea B. Montalvo:** Conceptualization (supporting); Methodology (supporting); Project administration (supporting); Supervision (supporting); Writing – review and editing (equal). **Toby J. Hibbitts**: Conceptualization (supporting); Formal analysis (supporting); Methodology (supporting); Project administration (supporting); Supervision (lead); Writing – review and editing (equal).

Transparent peer review

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Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.hmgqnk9zm (Kiel et al. 2026).

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